

A REVIEW OF THE *LITORIA NANNOTIS* SPECIES GROUP,
AND A DESCRIPTION OF A NEW SPECIES OF *LITORIA* FROM
NORTHERN QUEENSLAND, AUSTRALIA (ANURA: HYLIDAE)

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ABSTRACT

The identity of *Hyla dayi* Günther was discussed and re-examined in the light of extensive study on taxonomy and biology of northern Queensland frogs. It is proposed that the original description of *Hyla dayi* was based on a northern Queensland *Nyctimystes*. *Litoria dayi* non Günther is described and is named *rheocolus*.

A new species of *Litoria* from northern Queensland similar to *rheocolus* and *nannotis* is described, and is named *nyakalensis*. Tadpoles of *rheocolus* and *nannotis* are described, and the male calls of *rheocolus* and *nyakalensis* are discussed.

Litoria nannotis species group consists of three species, *rheocolus*, *nyakalensis*, and *nannotis*, all restricted to northern Queensland. Phylogenetic relationships amongst these three species are discussed; it is proposed that *rheocolus* is the most primitive, *nannotis* the most specialized, and *nyakalensis* is intermediate and probably the immediate ancestral stock of *nannotis*. It is suggested that the *Litoria nannotis* species group evolved in northern Queensland from a New Guinean ancestral stock which crossed the Torres Strait land bridge in the Pleistocene.

During the course of taxonomic and biological studies on northern Queensland frogs I collected an undescribed *Litoria* which is closely related to *Litoria dayi* auctorum and *Litoria nannotis*. Because little is known on the biology of the above species group, the doubtful identity of *Hyla dayi* Günther, and erroneous description of *nannotis* tadpole, it is desirable to review the whole species group which occurs in northern Queensland.

MATERIALS AND METHODS

Observations and drawings were carried out under a Wild stereoscopic microscope. Techniques and abbreviations of measurements not given in an earlier paper (Liem and Hosmer, 1973), are as follows: interorbital width (IO) is the narrowest width of the fronto-parietal, upper eyelid width (EW) is the widest section of the upper eyelid, tympanum width (TW) is the width of the tympanum measured along its horizontal diameter, and eye diameter (ED) is measured along its horizontal diameter. DSL is abbreviation for David S. Liem collection, and QM for Queensland Museum collection.

SYSTEMATICS

KEY TO SPECIES OF THE LITORIA NANNOTIS SPECIES GROUP

1. Head rounded; IN/EN ratio more than 0.970; web on 1st toe on or just beyond proximal subarticular tubercle; ventral surfaces of posterior portion of body cream with reddish brown tinge *nyakalensis*
Not as above 2
2. Snout shorter than eye diameter; snout bluntly rounded; loreal region strongly concave; prepollex enlarged; nuptial pad large with coarse spinules; single outer metacarpal tubercle; adult more than 40 mm in SV length *nannotis*
Not as above *rheocolus*

***Litoria rheocolus* sp. nov.**
(Figures 1, 4C, D; Plate 3A)

Hyla dayi (non Günther, 1897): Loveridge, 1935, p. 38; Copland, 1957, p. 20; Tyler, 1968, p. 502.

HOLOTYPE: Adult male, QM J22631 from Kuranda, 50 km west of Cairns, N. Queensland, collected 21 May 1972 by David S. Liem.

PARATYPES: 15 ♂—QM J22632–4, DSL 6187, 6588, collected together with the holotype; QM J22635–9, from Bloomsfield Rd, 50 km SE. of Cooktown, collected 14 October 1972; QM J22640–42 from Cape Tribulation, 100 km N. of Cairns, collected 11 October 1972; DSL 6522 from Henrietta Creek, Palmerston N. P., collected 17 October 1972; DSL 6517 from the Boulders, 5 km W. of Babinda, collected 10 October 1972.

5 ♀—QM J22643–4 from Cape Tribulation, collected 11 October 1972; QM J22645, DSL 6547, 6554 from Shiptons Flat, 50 km S. of Cooktown, collected 14 October 1972; all localities are in N. Queensland; all specimens were collected by David S. Liem.

OTHER MATERIAL: 56 specimens—Amos Bay, 45 km S. Cooktown, QM J22383–86; Shiptons Flat, 50 km S. Cooktown, QM J17848; Bloomsfield Rd, 55 km S. Cooktown, QM J17847, DSL 6536–8, 6540, 6542–3, 6545, 6550–2; Cape Tribulation 100 km N. Cairns, DSL 6176, 6181, 6191, 6548, 6527, 6530–1, 6533; Kuranda, 50 km W. Cairns, DSL 6606, 6173, 6175, 6178–80, 6183, 4925–30; Davies Creek Rd, 15 km SE. Mareeba, QM J18031; Tinaroo Creek Rd, 10 km SE. Mareeba, DSL 4932; Millaa Millaa Falls, DSL 6532–4; Henrietta Creek, Palmerston N. P., DSL 6518–21, 6523–4; The Boulders, 5 km W. Babinda, DSL 4839–45, 6514–16. Eleven tadpoles at stage 25 from Kuranda, 50 km W. of Cairns. All localities are in N. Queensland.

DIAGNOSIS: A moderate sized treefrog, ranging from 27.0 to 37.8 mm in SV length. It could be distinguished from *nyakalensis* and *nannotis* by the following combination of characters: 1, snout bluntly pointed; 2, prepollex normal, not enlarged; 3, nuptial pad small, spinules fine; 4, forearm of males normal, not robust; 5, webbing on outer margin of 3rd finger reaches base of penultimate phalanx. Furthermore it differs from *nyakalensis* by its narrow IN/EN ratio (less than 0.970), cream ventral surfaces without reddish brown tinge, and from *nannotis* by its smaller size (adults less than 40 mm), two outer metacarpal tubercles, snout larger than eye diameter, absence of keratin spinules on chest of males, and the males call.

DESCRIPTION OF HOLOTYPE: SV length 30.6 mm; TL 16.8 mm, 0.549 of SV length;

HW 11.0 mm, 0.359 of SV length; EN 3.3 mm; IN 3.0 mm; IN/EN ratio 0.909; IO 3.1 mm; EW 2.6 mm; IO/EW ratio 1.192; TW 1.5 mm; ED 3.1 mm; TW/ED ratio 0.405.

Tip of snout bluntly pointed; canthus rostralis sharp, angular in cross-section; loreal region slightly concave; dorsal view of head bluntly pointed (Fig. 1C), rounded blunt in profile (Fig. 1E); tympanum small; supratympanic fold present; tongue subovate, slightly nicked posteriorly; vomerine teeth in short, slightly oblique, oval rows just behind the level of the posterior edge of the choanae; upper jaw toothed; males without vocal sac.

Forearm not robust; a row of whitish tubercles present on lateral edge of forearm; distal segment of fingers expanded into disc; with ventro-marginal groove; 3rd finger disc larger than the diameter of the tympanum; length of fingers from shortest to longest 1-2-4-3; phalangeal formula of hand 2-2-3-3; basal segment of 1st finger not enlarged and its disc moderate in size; subarticular tubercles roundish, one each on 1st and 2nd fingers, and two each on 3rd and 4th fingers; two small supernumerary tubercles on base of metacarpal of 3rd and 4th fingers; two oval (small medial and an elongated lateral) outer metacarpal tubercles on base of the palm, and an elongated inner metacarpal tubercle on the proximo-ventral inner surface of the metacarpal of 1st finger.

Fingers moderately webbed: between 1st and 2nd fingers free of web; web between 2nd and 3rd fingers reaching just beyond the proximal subarticular tubercle by a narrow fringe; webbing between the two outer fingers reaching by a narrow fringe the 2nd subarticular tubercle of 3rd finger, and just beyond the 2nd subarticular tubercle of 4th finger. Nuptial pad small, and consists of small fine darkbrown keratinous spinules.

Hindlimbs moderately long; distal segment of toes expanded into disc, with a ventro-marginal groove; length of toes from shortest to longest 1-2-5-4-3; phalangeal formula of foot 2-2-3-4-3 subarticular tubercles roundish, one each on 1st and 2nd toes, two each on 3rd and 5th toes, and three tubercles on 4th toe; a row of minute supernumerary tubercles is present on metatarsal of 5th toe; an oval inner and a small round outer metatarsal tubercles are present; foot webbing reaching base of disc of 1st toe, outer margins of 2nd and 3rd toes, and inner margin of 5th toe; web reaches by a narrow fringe the base of disc of 2nd and 3rd toes; web reaches halfway down the penultimate phalanx of 4th toe.

Cloacal opening at mid-level of the thighs; skin of dorsum shagreen, with small conical tubercles scattered on the head, upper eyelids, pectoral region, and throat; postero-ventral portion of femur granular; skin fold across chest absent. Pupil horizontal, roundish to oval; palpebral venation on lower eyelid absent.

Colour: In life, dorsal colour slate; proximal portion of thighs dirty brown; sides of body greyish brown; ventral surfaces of throat, body and anterior portion of thighs cream without pinkish tinge; palm of hands, ventral surfaces of tarsus, plantar surfaces of foot brownish slate; posterior and postero-ventral of femur, and postero-ventral of upperarm slate tinge with tan; margins of throat lightly spotted with brown. In preservative, dorsal colour slate, brownish tinge not distinct, and ventral surfaces cream white.

DESCRIPTION AND VARIATION: There is no marked difference amongst the males: fourteen male paratypes are 28.9–32.4 mm in SV length (mean 30.85 ± 3.981 mm); TL/SV 0.522–0.589; HW/SV 0.330–0.389; IN/EN 0.867–0.968; IO/EW 1.000–1.270.

Male paratypes and other male specimens have similar finger webbing as the holotype; web between the two outer fingers reaching on or just barely touching the 2nd subarticular tubercle; web on outer margin of 3rd finger reaches approximately two thirds down the length of the proximal phalanx in 5 specimens (DSL 6183, 6173, 6175, 6178, and 4930). Foot webbing is slightly variable: toe webbing in the majority of males examined reaches just the base of disc on outer margin of 2nd and 3rd toes.

Females are larger than males: nine females including the paratypes ranging from 32.7–37.8 mm in SV length (mean 34.01 ± 2.181 mm); TL/SV 0.534–0.569; HW/SV 0.320–0.365; IN/EN 0.882–0.970; IO/EW 1.067–1.147. In some females the toe webbing is less extensive, e.g. in two specimens it reaches outer margin of 3rd finger approximately two-thirds down the length of the proximal phalanx, and in two others the web reaches three-quarters the length of the proximal phalanx of the 1st toe. In females the supernumerary tubercles of palm and sole are distinct, arranged in rows along the metacarpals and metatarsals; inner and outer metatarsal tubercles are small and rounded. In two females (DSL 6525–26) the conical tubercles on back are large.

Colour: In life most males have similar colouration as the holotype; in some males however (QM J22635, J22637–8, J22642), the fore and hindlimbs are dark grey with brownish tinge. In QM J22632, J22642, the dorsal colour is brownish with a vague broken inverted triangular marking; in others (QM J22633, and DSL 6522) the fore and hindlimbs are greyish with distinct dark spots; ventral surfaces of hands and feet are grey with dark markings. In preservatives the following specimens are ashy grey dorsally: QM J22643–4, J22641, DSL 4927, and 4930. In life the ventral surfaces of body and throat are spotted with brown pigments or lightly dusted on margins of throat.

Female colouration differs from the male; dorsal background colour brownish tan with a distinct black inverted triangular marking on the back, stretching from between the eyes down to the coccygeal region; dorsal surfaces of fore and hindlimbs are brownish or grey, spotted with dark pigments, or with irregular vague cross-bands; background colour of ventral surfaces cream; throat, pectoral region, antero- and postero-ventral surfaces of thighs heavily dusted with dark brown pigments; one individual (QM J22644) has a uniform cream whitish ventral surface dusted with greyish-brown on postero-ventral surfaces of the thighs.

MATING CALL: Regular repeated long drawn single note call, easily distinguished from the rasping call of *nyakalensis*. Details of the call structure will be reported elsewhere.

LIFE HISTORY: Amplexus pairs were observed from November to March; males call throughout the year except during cold winter nights; amplexus axillary. Males call from rocks or boulders in creeks or from vegetation overhanging water along streams and creeks. Eggs pigmentless, ovidiameter 1.4–1.8 mm; eggs are laid in compact gelatinous clumps under rocks in water.

Tadpoles at stage 25 ranging from 21.1–29.0 mm in snout-tail length (ST); tail height (TH)/tail length (TL) ratio 0.375–0.414; tail tip rounded; proximal half of dorsal and ventral tail fins are thick, and taper off posteriorly; muscular tail strong, and it is twice the height of the tail fins at base of tail (Fig. 4C); labia expanded and forms a large sucker-mouth (Fig. 4D); mouth width (MW)/body length (BL) ratio 0.512–0.702; the sucker-

mouth consists of two continuous rows of labial papillae, one row along the edges of the labium, and another one on the inner surface of the mouth close to the labial tooth rows; additional labial papillar rows are present on the posterior portion of the labia, and at the anterior angles of the mouth (Fig. 4 D). Labial teeth consist of two entire upper and three entire lower labial tooth rows (II/III); the inner rows are stronger than the outer rows.

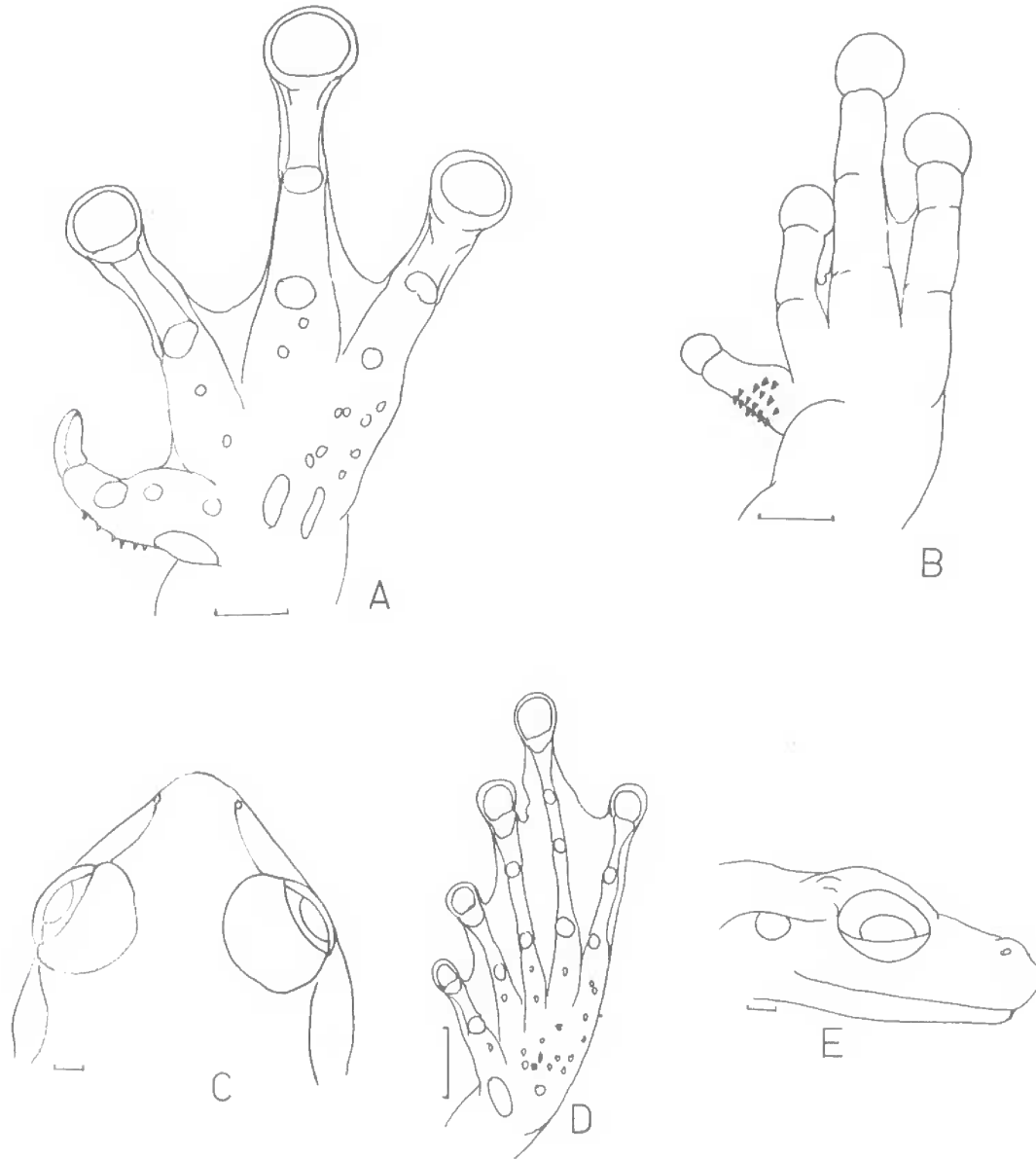


FIG. 1: *Litoria rheocolus*. A, ventral surface of hand (DSL 6187); B, dorsal surface of hand (DSL 6518); C, dorsal surface of head (DSL 6157); E, ventral surface of foot (QM J22645); F, lateral view of head (DSL 6517). Line equals 1 mm.

Upper jaw M-shaped; the lower jaw is V-shaped; both jaws are serrated (Fig. 4 D); spiracle opens at the end of a tube on ventro-lateral side of the body; anal opening median.

In life, body ground colour sandy; abdomen black and body darkbrown; the tail is transparent with reddish tinge; muscular tail lightly dusted with pale brown pigments. There is no marked differences between *rheocolus* and *nannotis* tadpoles.

Tadpoles live in fast flowing water current and are difficult to remove when clinging on rocks or other substrates. Efficient adaptation to fast water current is shown structurally by the large sucker-mouth, flattened head and body, and the strong muscular tail.

HABITAT: *Litoria rheocolus* is restricted along rocky fast flowing creeks and streams in rainforest as well as in wet sclerophyll forest. It ranges from sea level (Cape Tribulation and The Boulders) up to 1200 m above sea level (Mt. Lewis). This species is synchronopatric with *Litoria nyakalensis*, *nannotis*, *eucnemis*, *lesueuri*, *chloris*, and *infrafrenata*, *Nyctimystes hosmeri*, *tympanocryptis*, *Mixophyes schevili*, *Taudactylus acutirostris*, *rheophilus*, *Hylarana daemeli*, *Sphenophyrne phuvialus*, *Cophixalus ornatus* and *exiguus*.

DISTRIBUTION: It is distributed throughout the rainforest and wet sclerophyll forest from Palmerston N.P. (near Innisfail) in the south of Mt. Finigan (S. of Cooktown) in the north. *L. rheocolus* has yet to be discovered along the Cape York Peninsula rainforest chain.

ETYMOLOGY: The specific name is derived from the Greek *rheos* meaning creek or stream, and the latin suffix, *colus* meaning an inhabitant; it refers to the habitat of the frog.

DISCUSSION

In 1897 Günther described and named a treefrog *Hyla dayi* from a single specimen collected from Mt. Bartle Frere, northern Queensland by W. S. Day. The type probably lodged in the Tring Museum is now apparently lost (Tyler, 1968; H. G. Cogger and A. G. C. Grandison, *in litt.*).

Loveridge (1935) and Copland (1957) each refer one specimen collected to this species, and both add degrees of variation to the original description. Straughan (1966), studying 16 specimens, accepted Copland's modified description but noted variable webbing between fingers. Tyler (1968) using Loveridge and Copland specimens designated these *Hyla dayi* (Günther) whilst noting that they differed from the original description in extent of finger webbing, tympanum size, SV length and dorsal colouration—differences which he considered unimportant.

Included in a collection of practically all known northern Queensland frogs made personally during the past few years are approximately 50 specimens which correspond with *Hyla dayi* of Loveridge (1935), Copland (1957), Straughan (1966), and Tyler (1968), but careful examination convince me that these are not *Hyla dayi* Günther. The specimens studied come from various localities in northern Queensland, as far south as Mt. Spec, north of Townsville, and as far north as Mt. Finigan, south of Cooktown, and included specimens from part of Mt. Bartle Frere close to the type locality of *Hyla dayi* Günther. Specimens came from as low as sea level up to approximately 1000 m above sea level.

Distribution of characters which were used in the original description of *dayi*, amongst the small-eared northern Queensland treefrogs are presented in Table 1. As seen from

Table 1, SV length, dorsal colouration, and finger webbing are important and critical in establishing the status of the original description of *dayi*.

It is unfortunate that Günther (1897) did not define exactly the extent of webbing on the 3rd finger; he did not specify whether it reaches the base or the distal end of the penultimate phalanx of the 3rd finger. From his statement 'fingers strongly webbed', apparently the web on the 3rd finger extends beyond the base of the penultimate phalanx, probably close to the distal end. If this is true then the web of *dayi* holotype differs from *dayi* auctorum, but is similar to *Nyctimystes*. Live or preserved specimens of *dayi* auctorum, *nannotis*, and the undescribed *Litoria* are slate or olive with dark markings, but never uniformly brown. Females of *dayi* auctorum are brown dorsally, but they always have a distinct large inverted triangular black marking which extends from the level of the eye to the coccygeal region; Loveridge's (1935) specimen has a similar pattern and most likely it is a female. Amongst northern Queensland small-eared treefrogs, only females of *nannotis*, *Nyctimystes hosmeri* and probably also of *tympanocryptis* reach more than 50 mm in SV length. SV length of *dayi* holotype is substantially larger than *dayi* auctorum. Although *dayi* holotype is within the size range of *nannotis* females, they differ in other respects (see Table 1). Although texture of skin depends on the state of preservation, I believe that the large tubercles of *dayi* auctorum should have been detected were they present on the holotype.

Based on the above evidence I am convinced that *dayi* holotype was based on a *Nyctimystes* female; since uniform brown colour variant is present in *tympanocryptis*, *hosmeri* and *vestigea*. (The validity of *vestigea* is discussed by Liem, in MS). This makes specific identification impossible.

***Litoria nyakalensis* sp. nov.**

(Figure 2 ; Plate 4)

HOLOTYPE: Adult male, QM J22624 from Henrietta Creek, Palmerston N. P., N. Queensland, Australia, 800 m above sea level, collected 17 October 1972 by David S. Liem.

PARATYPES: Nine males, QM J22625–8, DSL 6502, 6719 collected together with the holotype: QM J22629–30, DSL 6174, collected 29 November 1971 from Beatrice Creek, Palmerston N. P., N. Queensland. All specimens were collected by David S. Liem.

OTHER MATERIAL: Besides the type series, two other specimens from Beatrice Creek, Palmerston N. P. were studied (DSL 4320–1).

DIAGNOSIS: A moderate sized robust treefrog, males ranging from 29.7–32.3 mm (mean 31.6 ± 2.975 mm) in snout-vent length. It could be distinguished from *rheocolus* and *nannotis* by the following combination of characters: 1, snout rounded; 2, IN/EN ratio more than 0.980; 3, first finger enlarged, its disc small; 4, web on 1st toe on or just beyond the proximal subarticular tubercle; 5, inner tarsal fold absent or indistinct; 6, ventral surfaces of forearms, hindlimbs, and part of the pectoral region are washed with reddish pink; 7, males have a rasping call. It is distinguished from *rheocolus* by the robust forearms, and large nuptial pad with coarse spinules; from *nannotis* by the smaller size (less than 40 mm in SV length), longer snout (snout longer than eye diameter), two outer metacarpal tubercles present, moderate sized prepollex, absence of keratinous spinules on chest, throat, and sides of head, and the males call.

DESCRIPTION OF HOLOTYPE: SV length 32.3 mm; TL 17.5 mm, 0.542 of SV length; HW 12.0 mm, 0.372 of SV length; EN 3.4 mm; IN 3.1 mm; IN/EN ratio 0.912; IO 3.5 mm; EW 3.0 mm; IO/EW ratio 1.167; TW 1.4 mm; ED 3.9 mm; TW/ED ratio 0.359.

Tip of snout rounded; canthus rostralis rounded in cross-section and it is distinct (Fig. 2A); loreal region slightly concave; dorsal view of head rounded; it is bluntly rounded in profile (Fig. 2C); tympanum small, partly hidden under the skin; supratympanic fold present; tongue subovate, free posteriorly; vomerine teeth in a lightly oblique short oval rows just behind the level of the choanae; vocal sac absent; upper jaw toothed.

Forearm robust; a row of whitish tubercles is present on lateral edge of the forearm; distal segment of fingers expanded into large disc, with ventro-marginal groove; length of fingers from shortest to longest 1-2-4-3; phalangeal formula of hand 2-2-3-3; first finger enlarged, but its digital disc is small (Fig. 2D). Fingers slightly webbed: web between 2nd and 3rd fingers reaches the proximal subarticular tubercles; web between 3rd and 4th fingers reaches halfway down the proximal phalanx of 3rd finger, and the 2nd subarticular tubercle of 4th finger by a narrow fringe. Nuptial pad large with coarse black keratinous spinules (Fig. 2B); subarticular tubercles roundish, one each on 1st and 2nd fingers, and one each on 1st and 2nd fingers, and two each on the two outer fingers; a row of supernumerary tubercles is present on metacarpal of 3rd and 4th fingers; a pair of outer metacarpal tubercles are present on the proximo-lateral portion of the palm, and an elongated tubercle on the proximo-ventral surface of the metacarpal of the 1st finger (Fig. 2D).

Hindlimbs moderately long; distal segment of toes expanded into disc, with ventro-marginal groove; length of toes from shortest to longest 1-2-5-4-3; phalangeal formula of foot 2-2-3-3; one subarticular tubercle each of 1st and 2nd toes, two each of 3rd and 5th toes, and three on the 4th toe; supernumerary tubercles are present on ventral surfaces on metatarsal of toes; inner metatarsal tubercle oval; outer metatarsal tubercle indistinct or absent. Toes extensively webbed; web reaches halfway down the proximal phalanx of 1st toe by a narrow fringe; web reaches just below base of discs on outer margins of 2nd and 3rd toes, and it reaches by a narrow fringe the proximal subarticular tubercle of 2nd toe, and the 2nd subarticular tubercle of 3rd toe; web reaches the 3rd subarticular of 4th toe; it reaches the base of the disc of 5th toe.

Cloacal opening at mid-level of the thighs; skin of dorsum with conical tubercles, scattered on the head, upper eyelids and back; dorsal surfaces of fore- and hindlimbs smooth with some scattered tubercles on tibia and heels; ventral surfaces of abdomen, chest, throat, and posterior ventral portion of the thighs granular; skinfold across chest absent.

Pupil horizontal, oval; palpebral venation on lower eyelid absent.

Colour: Dorsal colour of head and body slate; fore- and hindlimbs greyish brown, with indistinct dark markings; ventral surfaces of body and thighs cream, reddish pink on ventral surfaces of fore- and hindlimbs. Palm and sole uniformly grey to slate colour without dark markings.

In life, dorsum brownish olive or greyish brown with dark olive irregular markings on extremities; eyes brown with black pupil; ventral surfaces cream and reddish pink on fore- and hindlimbs as well as the pectoral region.

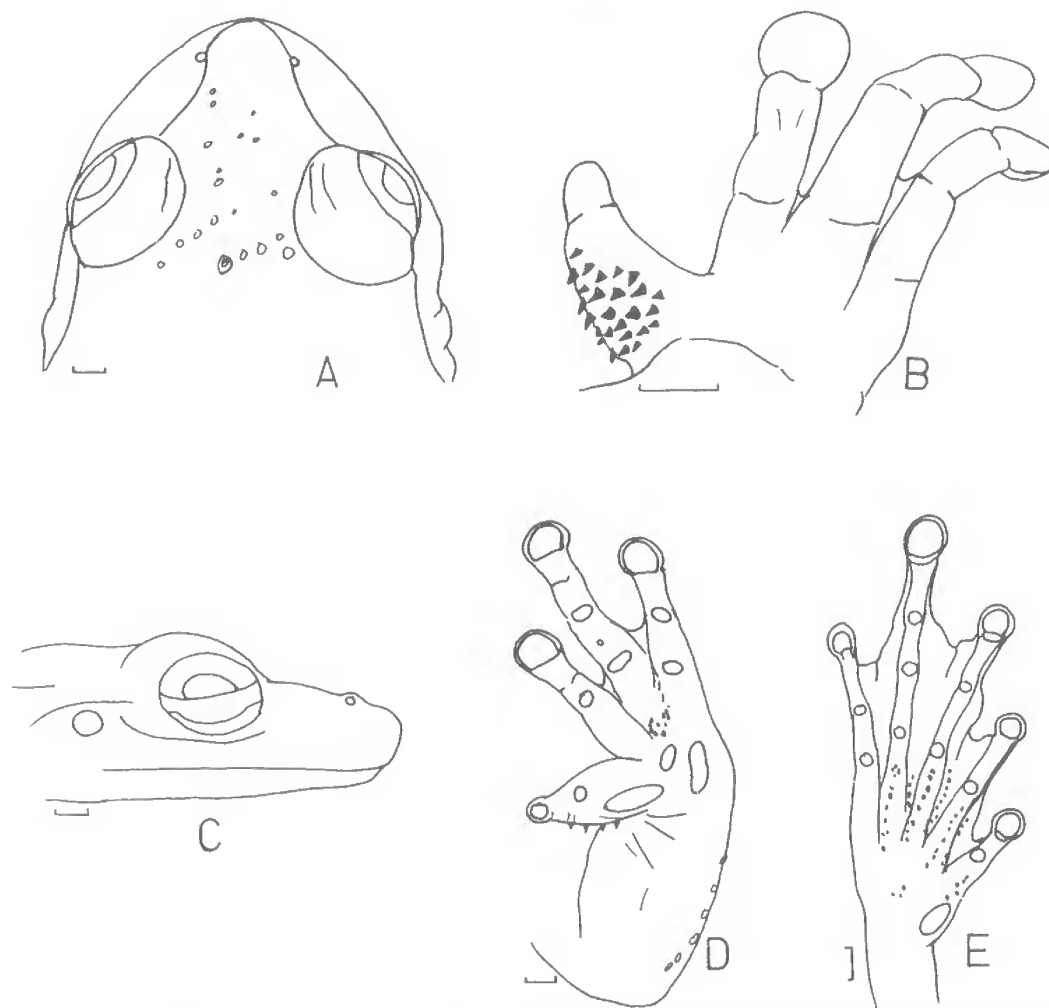


FIG. 2: *Litoria nyakalensis*. A, dorsal view of head (QM J22624, holotype); B, dorsal surface of hand (QM J22626); C, lateral view of head (QM J22624, holotype); D, ventral surface of hand (QM J22624, holotype); E, ventral surface of foot (QM J22625).

DESCRIPTION AND VARIATION: Six males from Henrietta Creek, Palmerston N.P. are 29.7–32.3 mm in SV length. Five males from Beatrice Creek Palmerston N.P., N. Queensland ranging from 30.8–33.1 mm in SV length. Because there is no marked differences between these two samples, their ratios are combined: TL/SV ratio 0.520–0.560; HW/SV ratio 0.330–0.377; IN/EN ratio 0.978–1.029; IO/EW ratio 0.999–1.133; TW/ED ratio 0.326–1.029.

There are slight variations in regard to the extend of finger webbing: in four specimens the web reaches only one-third down the length of the proximal phalanx on outer margin of 3rd finger, and not quite reaching the 2nd subarticular tubercle of 4th finger (QM J22629, J22625–6, DSL 6502). In QM J22625–7, J22629, DSL 4320–1, 6502, the web reaching the proximal subarticular tubercle of the 1st toe whereas in QM J22625–6, J22630, DSL 4320–1, 6502, the web barely reaches the base of disc on outer margins of 2nd and

3rd toes; in QM J22627 it reaches halfway down the penultimate phalanx of 3rd toe. in DSL 4320-1 the outer metatarsal tubercle is obscured, and in DSL 4320 the supernumerary tubercles of the foot area are absent or indistinct.

In life, the dorsal ground colour of *nyakalensis* varies from uniform slate colour to greyish brown, some specimens with dark irregular markings. In QM J22625-6 and J22628, the dorsal ground colour of fore- and hindlimbs are greyish brown, and is lighter than the dorsal colour of the body. In most individuals the ventral colouration is uniformly cream with reddish pink on forearm, pectoral region, thighs and tibia; in QM J22628-30, DSL 6174, 6502, 6719, the throat, pectoral region, lateral region of abdomen, antero- and postero-ventral surfaces of the thighs are heavily pigmented with brown markings washed with reddish brown pigmentation. The eye is brown, and with black pupil.

MATING CALL: Regular repeated rasping single note call, easily distinguishable from the long drawn single note call of *rheocolus*. Details of the call structure will be presented elsewhere.

LIFE HISTORY: Little is known about the life history of *nyakalensis*; mating call of males were heard from October to March. Females of this species are yet to be discovered, probably similar to *rheocolus* females. Tadpoles unknown; judging from the substantial similarities amongst the *Litoria nannotis* species group, *nyakalensis* probably has similar sucker-mouth tadpoles like the other two species.

HABITAT: *Litoria nyakalensis* occurs along creeks in rainforest and wet sclerophyll forest; it perches on rocks or on vegetation overhanging creeks. This species is synchronopatric with *Litoria rheocolus*, *eucnemis*, *lesueuri*, and *chloris*, *Nyctimystes tympanocryptis*, *Mixophyes schevili*, *Taudactylus acutirostris*, *Sphenophryne pluvialis*, *Cophixalus ornatus* and *exiguus*.

DISTRIBUTION: At present *L. nyakalensis* is known from three localities, Henrietta Creek and Beatrice Creek in Palmerston N.P., and Tinaroo Creek Rd, 15 km south of Mareeba, N. Queensland.

ETYMOLOGY: The specific name refers to Nyakali, an aboriginal tribal group who once lived in the vicinity of the type locality.

DISCUSSION

The new form of *Litoria* is intermediate between *rheocolus* and *nannotis*. In addition to characters listed in Table 1, the new form differs from *rheocolus* in the following respects: slightly larger IN/EN ratio, rounded snout, rounded canthus rostralis, first finger of males enlarged, moderate sized nuptial pad with large coarse spinules, males with robust forearm, less extensive webbing on 1st toe, and ventral surface cream with reddish brown tinge on posterior portion of the body.

It differs from *nannotis* by the smaller SV length, slightly larger IO/EN ratio, tympanum always distinct, slightly concave loreal, smaller prepollex in males, less extensive webbing on first toe, two outer metacarpal tubercles, and ventral surface cream with reddish brown tinge of posterior portion of the body. *Litoria nannotis* does not call; the rasping male call of the new form could readily be distinguished from the monotonous long drawn single note of *rheocolus*.

***Litoria nannotis* (Andersson)**
(Figures 3, 4 A, B; Plate 3B)

Hyla nannotis Andersson, 1916, p. 16; Tyler, 1965, p. 94.

Hyla obsoleta: Loveridge, 1935, p. 50 (part).

Hyla obsoleta nannotis: Copland, 1957, p. 55.

Litoria nannotis: Tyler, 1971, pp. 351, 353.

MATERIAL EXAMINED: (31) Shiptons Flat, 50 km S. Cooktown, QM J17861-3; Mt. Spurgeon, QM J5570; Mt. Lewis, 100 km N. of Cairns, DSL 5015-16; Tinaroo Creek Rd, 10 km SE Mareeba, DSL 4931; Atherton Tableland, QM J17017; Palmerston N.P., DSL 4261-2; Mt. Spec, 120 km N. of Townsville, DSL 4996-5001, 5003, 5005-10, 5012-14, 6198, 6306, 6343, 6559-60. All localities are in northern Queensland.

DIAGNOSIS: A moderately large sized treefrog, adult males ranging from 40.1-47.9 mm, and adult females from 49.1-54.7 mm in SV length. It differs from *rheocolus* and *nyakalensis* by the following characters: 1, short snout (shorter than eye diameter); 2, strongly concave loreal; 3, extremely enlarged prepollex; 4, keratin spinules are present on chest, margins of throat, and sides of head; 5, males do not call; 6, adults more than 40.0 mm in SV length; 7, only one outer metacarpal tubercle is present. It differs from *nyakalensis* by its smaller IN/EN ratio (less than 0.970), and it is further distinguished from *rheocolus* by its evenly rounded canthus rostralis.

DESCRIPTION OF HOLOTYPE: See Andersson (1916), and additional information in Tyler (1965).

DESCRIPTION AND VARIATION: Although Tyler (1965) gave an adequate account of variation, it is noteworthy to add more in the light of fresh material collected from new localities outside the range of published reports.

Males range from 40.1-47.9 mm in SV length; TL/SV 0.514-0.584; HW/SV 0.342-0.397; IN/EN 0.896-0.960; IO/EW 1.043-1.275; TW/ED 0.303-0.315 or obscured.

Females are larger: 49.1-54.7 mm in SV length; TL/SV 0.510-0.570; HW/SV 0.351-0.379; IN/EN 0.793-0.963; IO/EW 1.070-1.195; TW/ED 0.303-0.378 or obscured.

Tip of snout bluntly rounded; snout shorter than eye diameters; loreal region strongly concave; canthus rostralis evenly rounded in section; tympanum barely visible or hidden under the skin; tympanum is distinct in 6 (DSL 6560, 5000, 5015-16, 5010, 4996) out of 26 individuals studied. Only one large outer metacarpal tubercle is present (Fig. 3D); inner metacarpal tubercle on base of thumb elongated; prepollex extremely enlarged (Figs. 3D and E); supernumerary tubercles are present on palm, on metacarpals, and on the phalanges; a row of tubercles along lateral side of lower forearm present.

Fingers moderately webbed; web between 2nd and 3rd fingers reaching their proximal subarticular tubercles; web between 3rd and 4th fingers reaching halfway down the proximal phalanx of 3rd finger, and between half to three-quarters down the length of the proximal phalanx of the 4th toe.

Webbing of the foot reaching the base or barely reaching the base of disc of 1st, 2nd, 3rd, and 5th toes; it only reaches the 3rd subarticular tubercle (or just beyond it) of 4th toe (Fig. 3A); web on inner margins of 3rd and 4th toes reaches the base of discs by a narrow fringe; metatarsals are separated by webbing. Supernumerary tubercles are arranged in rows on the metatarsals; ventral surfaces of tarsus heavily tubercular; outer metatarsal

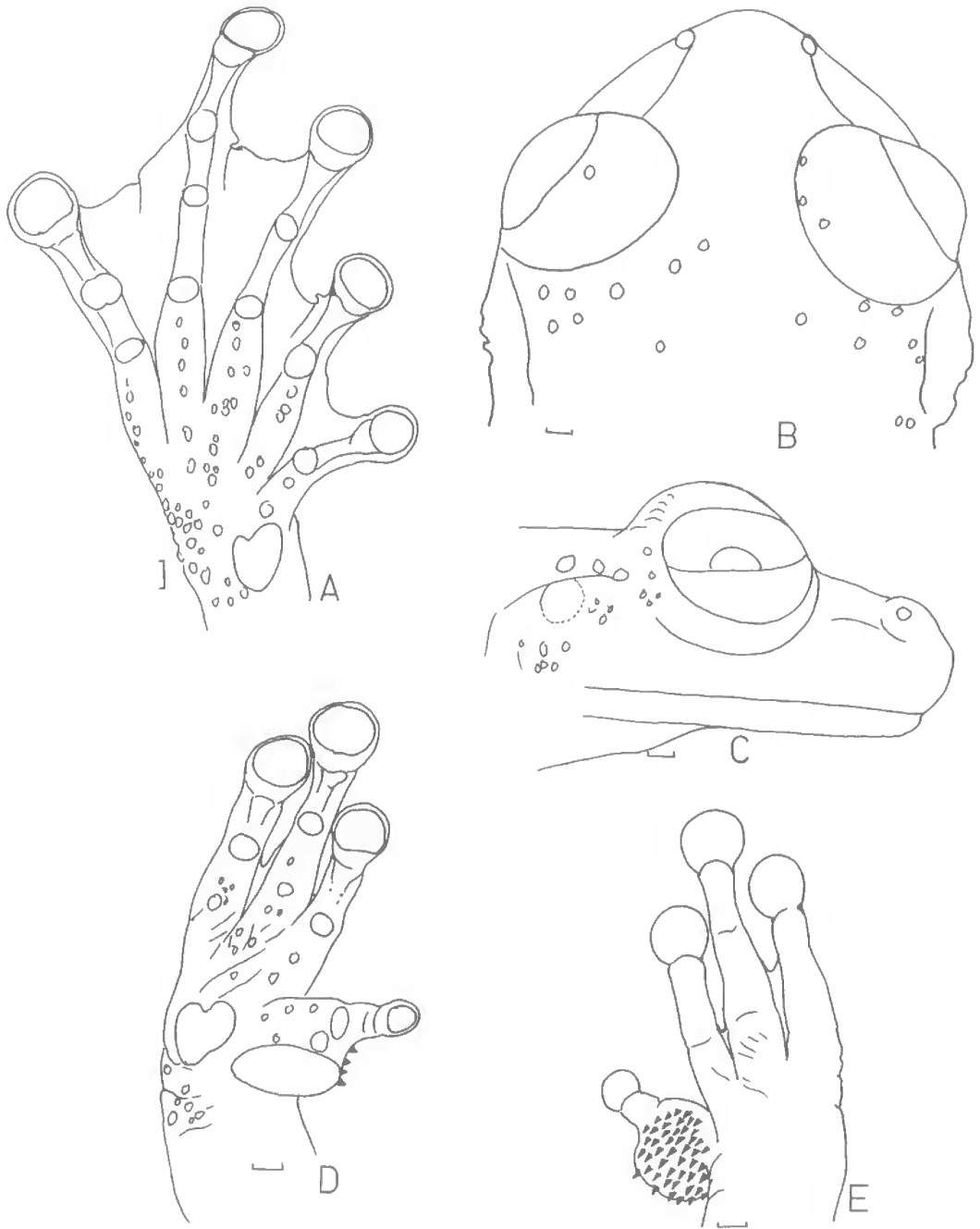


FIG. 3: *Litoria nannotis*. A, ventral surface of foot (DSL 5016); B, dorsal view of head (DSL 6960); C, lateral view of head (DSL 6960); D, ventral surface of hand (DSL 5016). E, dorsal surface of hand (DSL 5016).

tubercle small and rounded.

Tyler (1965) noted that in the holotype of *nannotis*, an internal vocal sac is present, but he failed to mention whether a vocal sac was present in other males. There is no trace of this vocal sac in any specimens examined. The report of the presence of a vocal sac in *nannotis* holotype is probably erroneous; short openings observed were probably artifacts.

Dorsal surface shagreen, with scattered tubercles on body, head and dorsal surfaces of the limbs; large tubercles are present on upper eyelids, posterior portion of eyes, tympanic region, on elbow and heel, on posterior and postero-ventral surfaces of the thighs. Ventral surfaces of the body (including the throat) are granular; only the anterior and antero-ventral surfaces of thighs, and inner surfaces of tibia and tarsus are smooth.

Adult males are easily distinguished from females by their smaller size, robust forearm, extremely large prepollex, heavily spinulated nuptial pad on the proximo-dorsal side of the thumb, and black tipped spinules on inner surfaces of forearm, base of forearm, along ventral and ventro-posterior region of the eyes, loreal region, and scattered on ventral surfaces of the thighs and inner surfaces of the tarsus.

Colour: In life, dorsal colour uniformly slate, or yellowish olive background with dark irregular markings (DSL 6343, 6559–60); in some individuals the extremities are washed with purplish colour (DSL 5010, 5005, 4997–8); dorsal colour of some individuals are pale slate (DSL 5000, 5007, 4999). Ventral surfaces of males cream; throat dusted with brown (DSL 6559, 6306, 5012). Ventral surfaces of females cream, and heavily pigmented with brown on the throat and ventral surfaces of the thighs; abdomen in four females (DSL 6343, 5000, 5014, 4999) is uniformly cream.

In preservatives the purplish brown colouration of the throat, ventral surfaces of fore- and hindlimbs disappeared; the majority of specimens are slate dorsally.

MATING CALL: No call has been associated to *nannotis*; males do not call.

LIFE HISTORY: Pigmentless eggs (ovidiameter 2.7–3.4 mm) are laid in gelatinous eggmasses under rocks in water. Eggmasses laid by amplexus pairs were raised, and hatched tadpoles were substantially different than those described by Tyler (1965), and Martin and Watson (1971). Large tadpoles described by Tyler (1965) were undoubtedly those of *Mixophyes schevili* (will be reported elsewhere); W. Hosmer (pers. comm.) who collected tadpoles (AMNH 67115) upon which Tyler (1965) based his description agreed that they were not *nannotis* but the common *Mixophyes schevili* tadpoles.

Tadpoles of *nannotis* are similar to *rheocolus*; the former have sucker-mouth, very strong muscular tail, and narrow tail fins (Fig. 4 A): spiracle opens at the end of a tube on ventro-lateral left side of the body; anal opening median. The sucker-mouth consists of two complete papillar rows, one along the edge of the labium, and another close to the labial tooth rows; the posterior half of the latter consists of a single row whereas its anterior half consists of two papillar rows; in addition to the above rows two or more rows of papillae are present on the posterior of the labium between the inner and outer rows (Fig. 4 B). The labial tooth row consists of two entire upper and three entire lower rows (formula II/III); the inner labial tooth rows are stronger than the outer ones. Jaws are strong, lower jaw is V-shaped, and the upper jaw is slightly indented anteriorly (Fig. 4 B).

In life, body ground colour sandy, with dark abdomen; tail with yellowish tinge and

numerous dark-brown blotches on muscular tail. Like *rheocolus* tadpoles they are highly adapted to fast flowing water current. Tadpoles of *nannotis* differ from *rheocolus* by their darker tail colouration and their yellowish tinge.

HABITAT: This species occurs along rocky fast flowing rainforest or wet sclerophyll forest creeks; *L. nannotis* is usually restricted near waterfalls. It is synchronopatric with *Litoria rheocolus*, *nyakalensis*, *eucnemis*, *lesueuri*, *infrafnata*, and *chloris*, *Nyctimystes hosmeri*, *tymanocryptis*, *Mixophyes schevili*, *Taudactylus acutirostris*, *rheophilus*, *Hylarana daemeli*, *Sphenophryne pluvialis*, *Cophixalus ornatus* and *exiguus*.

REMARKS: *Litoria nannotis* is restricted in rocky stream habitats with fast flowing water current, behind waterfalls. Unlike other frogs, adults and juveniles form a colony amongst large boulders behind waterfalls. These aggregations were observed during the day as well as at night. On various occasions I observed that individuals perch close together (sometimes on top of each other) in a corner of a boulder. Loud background noise of

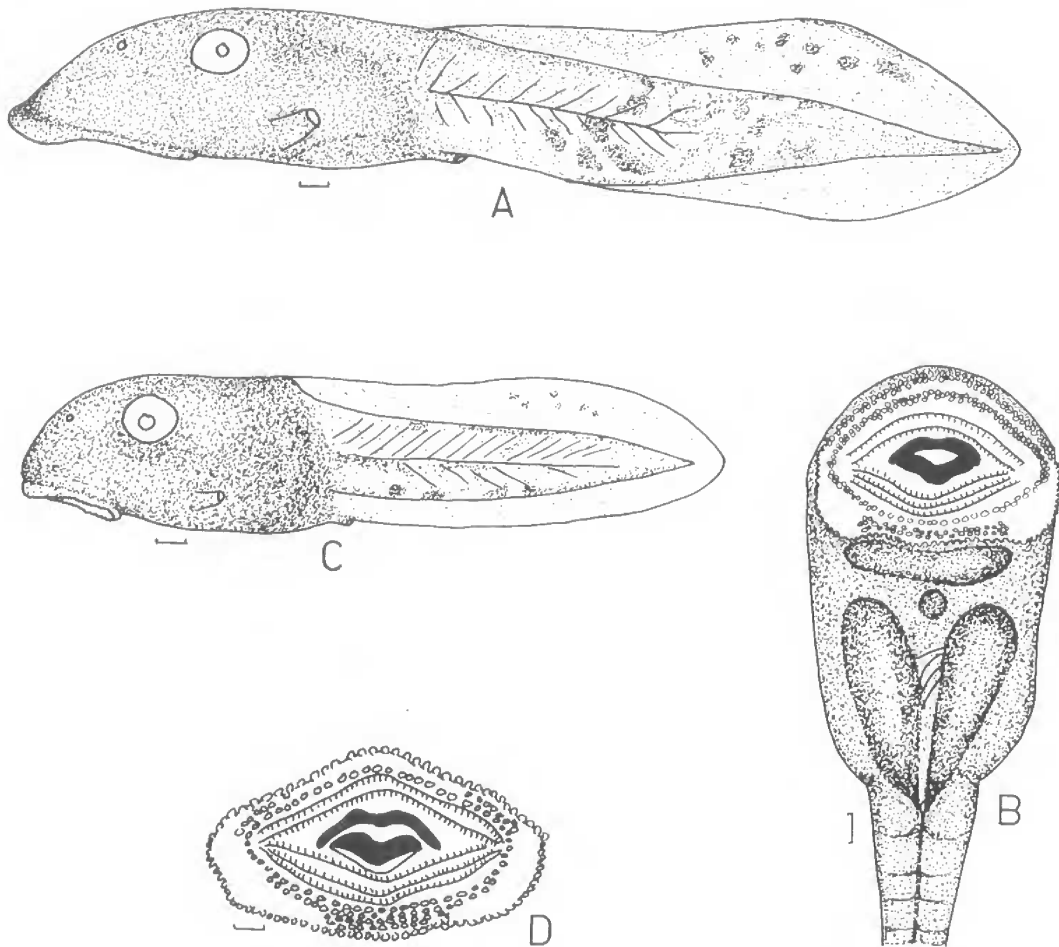


FIG. 4: A, B, *Litoria nannotis*. A, lateral view of tadpole, B, ventral view of body.
C, D, *Litoria rheocolus*. C, lateral view of tadpole. D, mouth parts.

rushing waterfall probably resulted in the loss of the male call; consequently colony aggregations keep males and females close together for breeding or social contacts. The large number of females collected in one place on Mt. Spec, suggests that females do not wander far from males and from their microhabitats behind waterfalls; large numbers of females collected at one spot is unusual in frogs.

DISTRIBUTION: Before the present study, *nannotis* was known only from the Atherton Tableland (Andersson, 1916; Loveridge, 1935; Copland, 1957; Tyler, 1965). My recent survey in northern Queensland reveals that it has a much wider distribution: it extends in the south to Mt. Spec (120 km NW of Townsville) and in the north to Mt. Finigan (50 km SE of Cooktown), N. Queensland. It is also found on Mt. Lewis, Mt. Spurgeon, Shiptons Flat, Tinaroo Creek Rd (15 km SW of Mareeba), Palmerston N.P., and Tully's Falls, all in northern Queensland. Its presence along the northeastern rainforest chain of Cape York Peninsula has yet to be discovered.

PHYLOGENETIC RELATIONSHIPS WITHIN THE *Litoria nannotis* SPECIES GROUP

Three species, *rheocolus*, *nyakalensis* and *nannotis* are placed in the *Litoria nannotis* species group. It is characterized by the following combination of characters: 1, moderate to large sized rheocolous treefrog; 2, tympanum small, less than 0.4 the width of eye diameter; 3, prepollex small to large; 4, moderate to very coarse nuptial pad spinules; 5, fingers moderately webbed—web on 3rd finger reaches base of penultimate phalanx or less; 6, vomerine teeth in short or long rows, behind level of choanae; 7, eggs unpigmented, individually encapsulated; 8, eggs laid in a clump under rocks in water; 9, sucker-mouth tadpoles with median anal opening; 10, labial tooth row formula II/III.

Satisfactory interpretation of phylogenetic relationships requires knowledge (or reasonable assumption) of primitive and derived states. This method had been used by Ozeti and Wake (1969), and Liem (1970, and MS). I adopted Marx and Rabb's (1970) criteria for establishing primitive and derived states.

Nine characters utilized for deducing phylogenetic relationships amongst species of the *Litoria nannotis* species group are presented in Table 2. The best phylogenetic tree obtained from these characters is presented in Figure 5 (construction of tree see detail in Liem, 1970 and MS). Even scanning through Table 2, it is obvious that *nyakalensis* shares more states with *nannotis* than with *rheocolus*, and this is shown by the best tree (Fig. 5). Based on the above evidence I consider *rheocolus* the most primitive, and the ancestral stock of *Litoria nannotis* species group; *nannotis* is the most specialized, whereas *nyakalensis* is intermediate between *rheocolus* and *nannotis*. *Litoria rheocolus* which is the most common and widely distributed species and lives in generalized creek habitats in contrast to the restricted waterfall microhabitat of *nannotis* or the restricted distribution of *nyakalensis*, lends support to the above hypothesis.

Relationships between *Litoria nannotis* species group and New Guinean species is unclear. Its restricted distribution in northern Queensland rainforest and wet sclerophyll forest, and its 'rheocolous' habits, strongly suggests that *Litoria nannotis* species group is a recent arrival into northern Queensland from New Guinea. Probably its ancestral stock crossed the last Torres Strait land bridge in the Pleistocene together with *Rana daemeli*, *Nyctimystes*, and other microhylids (Liem and Hosmer, 1973).

TABLE 1
DISTRIBUTION OF CHARACTER STATES OF *Hyla dayi* GÜNTHER, *Litoria dayi* (NON GÜNTHER), *L. nyakalensis* SP. NOV., *L. nannotis* (ANDERSON),
Nyctinystes tympanocryptis, (ANDERSON), AND *N. hosmeri* TYLER.

Character	<i>H. dayi</i> Günther	<i>L. dayi</i> non Günther	<i>L. nyakalensis</i> sp. nov.	<i>L. nannotis</i>	<i>N. tympanocryptis</i>	<i>N. hosmeri</i>
Tongue subovate, nicked	yes	yes	yes	roundish	yes	yes
Vomerine tooth row	transverse	slightly oblique	slightly oblique	long, transverse	transverse	transverse
Head depressed	yes	moderate	yes	no	yes	yes
Snout longer than eye	yes	yes	yes	no	yes	yes
Canthus rostralis	angular	angular	rounded	rounded	angular	angular
Loreal	straight	slightly concave	slightly concave	concave	straight	straight
IO broader than EW	yes	yes	yes	yes	yes	yes
TW/ED	0.250	0.357-0.430	0.326-0.410	indistinct/0.303-0.403	0.300-0.422	0.226-0.362
Fingers strongly webbed	yes	no	no	no	yes	yes
Web of 3rd finger	?	base of penultimate phalanx	‡ proximal phalanx	‡ proximal phalanx	‡ penultimate phalanx	base of penultimate phalanx
Toes fully webbed	yes	yes	yes	yes	yes	yes
Finger disc/tympanum	slightly smaller	smaller to larger	larger	larger	larger	larger
Inner tarsal fold	present	present	absent/indistinct	present	present	present
Dorsal skin	smooth	tubercular	tubercular	tubercular	smooth/shagreen	shagreen
Ventral skin	granular	granular	granular	granular	granular	granular
Supratympanic fold	present	present	present	present	present	present
Skin fold across chest	absent	absent	absent	absent	absent	absent
Ventral colouration	whitish	whitish cream	cream/reddish	cream with dark marking	cream white	cream white
Dorsal colouration	uniformly brown	males slate, females brown with black marking	slate	slate, olive with dark markings	brown, greyish-brown with/without spots	brown, grey with/without spots
SV length	52 mm	27.0-37.8 mm (N=60)	30.8-33.4 mm (N=12)	40.1-53.8 mm (N=29)	31.2-35.9 mm (N=39)	33.8-55.3 mm (N=39)

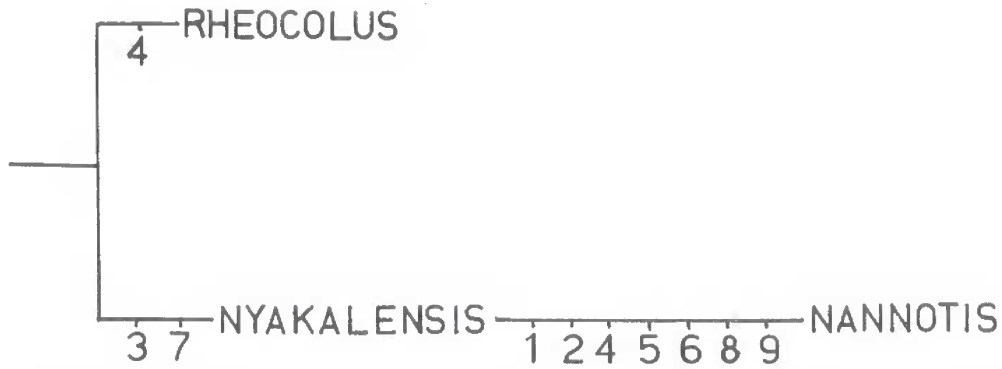


FIG. 5: Suggested phylogenetic tree of *Litoria nannotis* species group. Numbers along nodes are number of derived states (see Table 2).

TABLE 2
CHARACTER DISTRIBUTION OF *Litoria nannotis* SPECIES GROUP.

Character	Character State*	Species†
Snout	0, longer than eye 1, shorter than eye (1)	1, 2 3
Tympanum	0, distinct 1, indistinct or obscure (2)	1, 2 3
Canthus rostralis	0, angular 1, rounded (3)	1 2, 3
Inner tarsal fold	0, absent/indistinct 1, present (4)	2 1, 3
Outer metacarpal tubercle	0, two 1, one (5)	1, 2 3
Prepollex	0, moderate size 1, very large (6)	1, 2 3
Nuptial pad spinules	0, moderately fine 1, coarse (7)	1 2, 3
Chest keratin spinules	0, absent 1, present (8)	1, 2 3
Male call	0, present 1, absent (9)	1, 2 3

* Primitive state is coded 0 and the derived state 1. Numbers in brackets are derived states number and they are also used in the phylogenetic tree in Fig. 5.

† 1, *L. rheocolus*; 2, *L. nyakalensis*; 3, *L. nannotis*.

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PLATE 3

A: Holotype of *Litoria rheocolus* (QM J22631).

B: *Litoria nannotis* (DSL 5001).

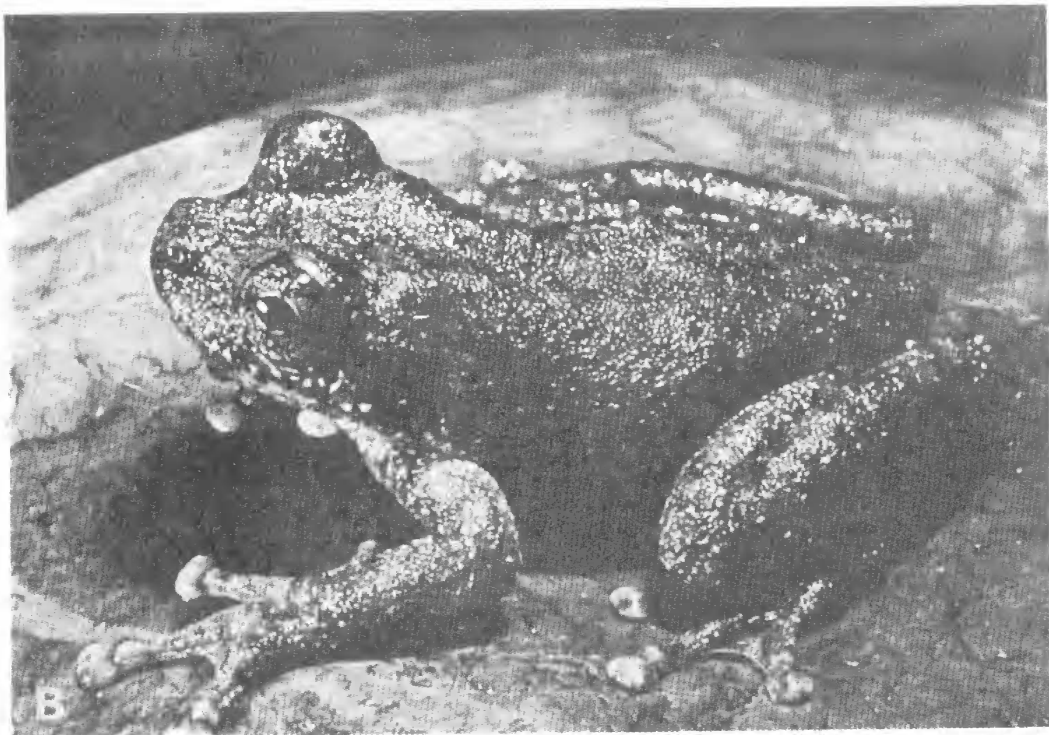
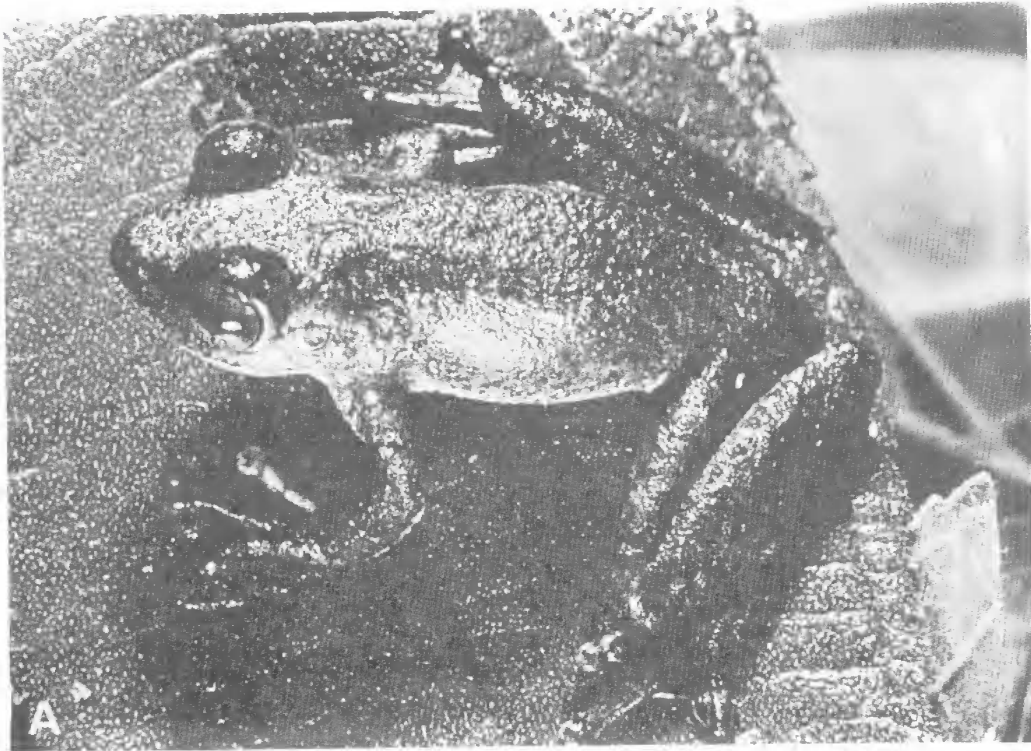


PLATE 4

Holotype of *Litoria nyakalensis* (QM J22624).

